

Turnover in the guild of larger carnivores in Eurasia across the Miocene-Pliocene boundary

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Abstract. There is considerable turnover of the mammalian fauna of western Eurasia from the Turolian to the mid-Villafranchian (MN 11 - 17; ca 8.5 - 2.0 Ma), particularly among the Carnivora where 31 of 34 species (92%) known from MN 13 are extinct by MN 14. This event affected all carnivore families and led to marked changes in guild structure. In MN 13 and earlier hyaenas had occupied niches for cursorial and semi-cursorial medium-sized scavengers. These species were replaced by canids, which had migrated to Eurasia from North America towards the end of the Miocene. Conical toothed cats, rare in the late Miocene, became more common from MN 14 onwards. The reason for these changes is not well understood, but they occur against a backdrop of continuous change in the physical environment that must have impinged on mammalian evolution in general. A major impediment to better understanding is the relative dearth of MN 14 faunas in western Europe, but the results of continuing studies of Mio-Pliocene mammalian faunas in China may help to address this problem.

Key words: Miocene, Pliocene, Carnivores, Eurasia, faunal turnover, guild structure

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I. INTRODUCTION

It has long been recognised that there is a considerable turnover in the terrestrial mammalian fauna of Europe at the Miocene-Pliocene boundary, with some 122 of the 178 known later Miocene genera failing to appear in the Pliocene (SAVAGE & RUSSELL 1983). This event is clearly marked among the Carnivora, in which in Europe alone a guild of 59 Late Miocene species is reduced to only 32 early Pliocene taxa according to the figures employed by those authors. More recent assessments of the later Miocene in western Eurasia have produced figures in broad agreement with those in of SAVAGE & RUSSELL (1983), with a mass extinction of 31 of 34 known species (92%) at the end of the Turolian (WERDELIN in press), while large scale extinctions are now known to take place in the fauna of the Yushe Basin of North China at around 5.0 Ma (FLYNN et al. 1991).

In this paper we seek to examine the nature of the Mio-Pliocene turnover in the guild of larger Carnivora within the larger setting of Eurasia. Although the quality of data falls off for this period as one moves eastwards, and the extent of provinciality that can be seen in western Eurasia cautions

Table 1

Faunal Turnover in Carnivora, Late Miocene – Early Pliocene, of Europe. Data from SAVAGE & RUSSELL (1983)

	Late Miocene	Early Pliocene taxa	Difference
<i>Ursidae</i>	8	4	-4
<i>Mustelidae</i>	20	11	-9
<i>Procyonidae</i>	1	1	0
<i>Canidae</i>	1	5	+4
<i>Hyaenidae</i>	15	3	-12
<i>Felidae</i>	14	8	6
<i>Total</i>	59	32	-27

us against treating the whole region as a monolith, it remains clear to us that any consideration of the larger patterns seen in Europe alone must consider the great landmass of Asia.

For reasons of practical convenience to do with space and with the current status of taxonomic revision and the density of the fossil record we shall concentrate on the Felidae, Hyaenidae and, to a lesser extent, the Canidae. The first two families in particular are by far the best known for this period, while the evolution of the Hyaenidae and the Canidae exhibit what we believe may be important features of guild structure. In contrast, the Mustelidae, while widely recorded, are often found in fragmentary state and are currently a taxonomic mess.

In terms of time scale, we shall draw on data from the period around 10.0 Ma to around 2.0. The equivalent European land mammal ages and the Neogene Mammalian zones relevant to this period are shown in Fig. 1.

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II. ENVIRONMENTAL BACKGROUND

The ever changing geography of Eurasia throughout the Miocene and into the Pliocene, driven by continued tectonic activity, ensured that the environment and habitat ranges of the mammalian fauna did not remain stable (RAYMO & RUDDIMAN 1992). Movements of the African and Indian plates against the Eurasian plate led to the eventual formation of the Alpine and Himalayan mountain chain and the Tibetan Plateau, and resulted in the gradual closures of the Paratethys and Tethys seaways (RÖGL & STEININGER 1983; WHYBROW 1984). Towards the end of the Miocene, the Messinian salinity crisis marked the isolation and evaporation of the Mediterranean, and with it the final severing of contact between it and the Indian Ocean, an event provoked by tectonic closure of the Gibraltar portal and one with its own profound influences upon climate (MÜLLER & HSÜ 1987, but see SUC & BESSAIS 1990). During the middle and early late Miocene provinciality of mammal faunas appears to have increased markedly, only to decrease again towards the end of the Turolian (FORTELIUS et al. in press).

The alterations to the physical environment had severe effects upon the biotic environment of Eurasia and North Africa. Cooler winters, coupled with decreased summer rainfall led to a gradual development of open woodlands, and the appearance of the Turolian land-mammal fauna is simply the latest stage in the evolution of a fauna with ever more emphasis on open-country taxa, as seen in the increasing numbers of hypsodont herbivores and omnivores present throughout the middle and late Miocene and in the specific adaptations to hypsodonty and cursoriality seen among equids,

Age (Ma)	Mn Units	Epoch	Faunal Unit
		E. Pleistocene	
2	MN17	Pliocene Late	Villafranchian
	MN16		Villanyian
3	MN15		
4	MN14	Pliocene Early	Ruscinian
5	MN13	Late Miocene	Turolian
6			
7	MN12		
8	MN11		
9			

Fig. 1. Late Miocene to Recent European mammal units and faunal ages.

bovids, giraffids and rhinocerotids (BERNOR 1984; FORTELIUS et al. in press). In the Siwaliks, where the incursion of species from elsewhere seems to have been an important factor in the evolution of local faunas (BARRY et al. 1985, 1990), open habitats with C₄ grasses appear to have expanded from about 9.0 Ma (MORGAN et al. 1994) and become established in the period between 8.0 and 5.0 Ma (QUADE et al. 1989; CERLING et al. 1989). By the very latest Miocene extensive steppe vegetation had begun to develop in Asia (TRAVERSE 1988). The immense richness of the later Miocene faunas of Eurasia can thus be seen as a direct reflection of the mosaic nature of the habitat distributions, with immigrants in the various regions simply adding to the existing structure rather than replacing the indigenous forms.

These trends towards vegetation and habitat diversity continued in some areas during the earlier Pliocene, particularly in western Asia and in parts of Europe around the Mediterranean where there was a shift towards seasonal aridity (TRAVERSE 1988). However, in other parts of western Europe there was something of a swing back towards warm-temperate forests, which is reflected in a number of elements of the Ruscinian fauna.

III. MIOCENE CARNIVORE TAXA

Figures 2-4 list the various Hyaenidae, Felidae and Canidae known from the late Miocene and early Pliocene of Eurasia. These figures highlight quite dramatically the reduction in diversity seen both within the later part of the Miocene and in the earliest Pliocene. In the case of the Hyaenidae, one notable feature of the Miocene fauna is the fact that most of the diversity is made up of taxa that exhibit rather canid-like dental adaptations and body plans, particular examples being among the genera *Ictitherium* and *Hyaenictitherium*, and insectivore/omnivore dental adaptations, seen in the genera *Plioverrops* and *Protictitherium*. These forms contrast markedly with the large-

Taxon	MN 11	MN 12	MN 13	MN 14-15	MN16-17
<i>Protictitherium llopisi</i>					
<i>Protictitherium crassum</i>					
<i>Protictitherium sumegense</i>					
<i>Protictitherium csakvareense</i>					
<i>Plioverrops orbignyi</i>					
<i>Plioverrops guerini</i>					
<i>Ictitherium viverrinum</i>					
<i>Hyaenotherium wongii</i>					
<i>Miohyaenotherium bessarabicum</i>					
<i>Hyaenictitherium hyaenoides</i>					
<i>Ictitherium pannonicum</i>					
<i>Hyaenictitherium parvum</i>					
<i>Lycyaena</i> sp.					
<i>Adcrocuta eximia</i>					
<i>Lycyaena chaeretis</i>					
<i>Hyaenictis graeca</i>					
<i>Hyaenictis almerai</i>					
<i>Palinhyaena reperta</i>					
<i>Belbus beaumonti</i>					
<i>Protictitherium</i> sp.					
<i>Ictitherium ibericum</i>					
<i>Plioverrops faventinus</i>					
<i>Chasmaporthetes borissiaki</i>					
<i>Chasmaporthetes lunensis</i>					
<i>Pliocrocuta perrieri</i>					
<i>Leecyaena bosei</i>					
<i>Crocuta crocuta</i>					
<i>Pachycrocuta brevirostris</i>					

Fig. 2. Late Miocene and early Pliocene Hyaenidae of Eurasia.

toothed, bone-smashing capabilities of the living taxa, as exemplified by *Crocuta crocuta*, the spotted hyaena. The only Miocene species to exhibit such adaptations to any marked extent is *Adcrocuta eximia*, one of the most wide ranging and long-lived hyaenids of the period, although something of a transitional morphology can be seen in *Palinhyena reperta* and *Belbus beaumonti* (WERDELIN & SOLOUNIAS 1991).

The contrast in numbers between the late Miocene and early Pliocene Felidae is equally marked (Fig. 3), and it becomes immediately apparent that the diversity of the Miocene Hyaenidae was simply part of an overall diversity within the guild at that time. Considerable size variation is evident between the Miocene felids, while the emphasis throughout tends to be on species with machairodont dentitions.

Taxon	MN 11	MN 12	MN 13	MN 14-15	MN 16-17
<i>Pseudaelurus turnauensis</i>					
<i>Machairodus aphanistus</i>					
<i>Paramachairodus ogygia</i>					
<i>Machairodus copei</i>					
<i>Epimachairodus romeri</i>					
<i>Stenailurus teilhardi</i>					
<i>Metailurus parvulus</i>					
<i>Metailurus major</i>					
<i>Felis attica</i>					
<i>Machairodus giganteus</i>					
<i>Paramachairodus orientalis</i>					
<i>Machairodus kurteni</i>					
<i>Machairodus irtyschensis</i>					
<i>Dinofelis</i> sp.				
<i>Homotherium latidens</i>					
cf. <i>Lynx</i> sp.					
<i>Megantereon cultridens</i>					
<i>Acinonyx pardinensis</i>					
<i>Panthera</i> sp.					

Fig. 3. Late Miocene and early Pliocene Felidae of Eurasia

The Canidae are unusual among the living Carnivora in being so widely dispersed in comparison with their restricted Miocene distribution (Fig. 4). From a North American origin point during the Oligocene they appear to have dispersed to Eurasia only during the later stages of the Miocene (MARTIN 1989), although the precise details of this initial Eurasian radiation remain obscure and the paraphyletic status of the genus *Canis* is strongly implied (WERDELIN in press). Taxonomic difficulties are compounded by the fact that the earliest Eurasian specimens are found in MN 12 and MN 13 deposits in Spain and Italy, and not in regions to the east.

Taxon	MN 11	MN 12	MN 13	MN 14-15	MN 16-17
<i>Canis cipio</i>					
' <i>Canis</i> ' sp.					
<i>Nyctereutes donnezani</i>					
' <i>Canis</i> ' sp.					
<i>Nyctereutes megamastoides</i>					
<i>Canis</i> sp.					
<i>Cuon</i> sp.					
<i>Canis falconeri</i>					
<i>Canis mosbachensis</i>					
<i>Canis arnensis</i>					

Fig. 4. Late Miocene and early Pliocene Canidae of Eurasia.

IV. PLIOCENE TAXA

Several of the Pliocene taxa appear equally long-lived, particularly the hyaenid *Pliocrocota perrieri* and the machairodont felids *Megantereon cultridens* and *Homotherium latidens*. It should be noted here that we consider *P. perrieri* to include material previously referred to the taxa *Pliocrocota pyrenaica* and *Hyaena prisca*, as discussed elsewhere (TURNER 1990, 1992; WERDELIN & SOLOUNIAS 1991). *Pliocrocota perrieri* has an odd distribution in Europe, where it disappears at around 1.7 Ma only to reappear again in the earlier part of the Middle Pleistocene, seemingly by a dispersion from Asia (TURNER 1992), where it is first recorded in the Gaozhuang Formation between 4.47 and 3.97 Ma (FLYNN et al. 1991). It is accompanied throughout the span of its first appearance in Europe by *Chasmaporthetes lunensis*, itself last recorded in earliest Pleistocene deposits at Olivola, although the dominance of these two is augmented during the Ruscinian in France and Moldavia by the appearance of the rather more primitive taxon *C. borissiaki*.

In Asia, Siwalik deposits contain material referred to *Leecyaena bosei*, although the precise generic home of this species remains unclear (WERDELIN & SOLOUNIAS 1991). The age of these deposits is equally uncertain, although they may belong to a broadly Ruscinian/Villafranchian span.

It is within Pliocene deposits that the first evidence is seen of *Pachycrocota brevirostris*, the largest of all the true hyaenas and one of the most extreme bone destroyers. Origins and precise first appearance are not entirely clear, although an early record of it (TURNER 1990), or at least a closely similar taxon (WERDELIN & SOLOUNIAS 1991), is known at around 3.0 Ma at the South African locality of Makapansgat. Elsewhere, it is not recorded in Europe until the earliest Pleistocene (TURNER 1992) and from Siwalik deposits of broadly similar age (TURNER in prep.), so that it is not at present to be seen as a significant component of the Mio-Pliocene turnover.

Homotherium is one of the most successful of the larger Pliocene and Pleistocene taxa, with a temporal and geographic distribution that encompasses Africa, Eurasia and North America. It first became extinct in Africa at about 1.5 Ma (TURNER 1990), but survived until around 0.5 Ma in Eurasia and until the Upper Pleistocene in North America. *Megantereon cultridens* is widely known in Pliocene and Lower Pleistocene deposits, but appears to have become extinct between around 1.0 Ma in western regions and 0.5 Ma to the east (TURNER 1987, 1992).

V. DISCUSSION

One of the most obvious features of the transition in the Eurasian Mio-Pliocene guild outlined above is the reduction in canid-like morphotypes among the Hyaenidae and the parallel rise in numbers and ecological importance of the Canidae. FLYNN et al. (1991) remark on this correlation in the context of the Yushe Basin, with the presence of what they simply refer to as "*Canis*" in earliest Pliocene deposits, while also noting that the disappearance of the large Miocene bone-crushing *Adcrocuta eximia* is matched by the first appearance of *Pliocrocota*. They also identify true *Canis* by about 3.0 Ma, although they point out that this appearance in China may have been by dispersion from Europe, and the slightly later appearance of *Cuon* in Haiyan Formation deposits dated between 2.5 and 1.9 Ma.

MARTIN (1989) has suggested that social hunting by packs is an entirely Plio-Pleistocene development, arguing that development of herding structure among herbivores is likely to have been one of the primary impetuses behind such a behavioural switch, and that such herding would only become prominent in more open terrain. It is certainly clear that the living *Crocota crocuta* displays its cooperative hunting abilities to best effect in such conditions (KRUUK 1972), while operating more individualistically in wooded areas (BEARDER 1977). The closed conditions of the Miocene, and the implied absence of cooperative action among the Hyaenidae of the period which is generally an ineffective strategy in woodland, is perhaps also reflected in the range of dental structures displayed, with only *Adcrocuta eximia* having the bone-smashing abilities of the modern species. Such abilities would only be of use to animals able to expropriate partially-eaten carcasses by weight of numbers. The postcranial skeleton of this animal shows that it was not a particularly cursorial species, perhaps reinforcing the idea that it was something of a specialist scavenger.

What we therefore see in the earliest Pliocene is the emergence of a differently organised guild, although its roots can clearly be traced back into the Miocene. The large cats, all machairodonts, are largely specialised as flesh-eaters dependent on seizing prey and holding it still while killing it in order to avoid (or at least minimise) damage to their canines. The hyaenas have started to show the specialised ability to demolish bone, and thus to obtain a consistent living from scavenging when necessary, although it is interesting to note that a second, major morphotype continues throughout the Pliocene in the form of the cursorial, so called hunting hyaenas of the genus *Chasmaporthetes*. The rise to prominence of the dogs seems to lag some way behind the demise of the canid-like hyaenas, but it means that by the end of the Pliocene the whole structure of the guild was organised more on modern taxonomic lines than was the case during the Miocene. After a period of some stability during the Pliocene these structural changes then continue during the Lower Pleistocene and culminate with the appearance of a thoroughly modern, somewhat eastern African-like guild by the Middle Pleistocene (TURNER 1992).

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